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Experiment Station**

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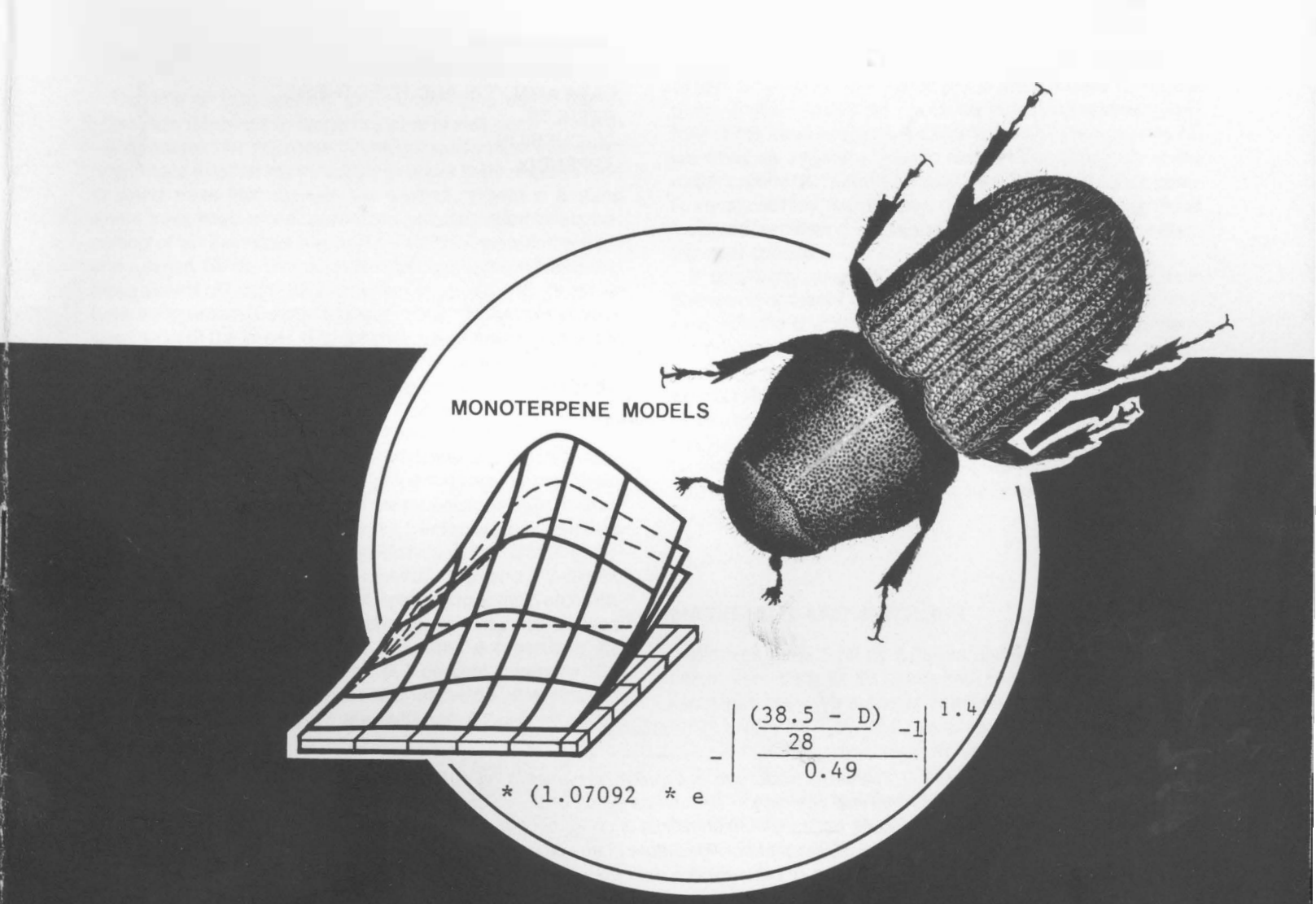
Monoterpenes of Lodgepole Pine Phloem as Related to Mountain Pine Beetles

Walter E. Cole, E. Park Guymon, and Chester E. Jensen



THE AUTHORS

WALTER E. COLE is Project Leader of the Population Dynamics of the Mountain Pine Beetle research work unit in Ogden, Utah. This unit was started in 1960 under his direction, as was the early research groundwork on the mountain pine beetle. Prior to this assignment, he did population dynamics research, control, and survey work on the spruce budworm and pine butterfly in southern Idaho. He did biological research and survey data collection on the spruce bark beetle in Fort Collins, Colorado. He began his career with Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, as supervisory control and survey aid in Berkeley, California. Dr. Cole has authored 31 publications.

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CHESTER E. JENSEN, retired, served as principal statistician for the Intermountain Forest and Range Experiment Station from 1967 to 1980. He held the same position at the Northeastern and Central States Forest Experiment Stations prior to coming to the Intermountain Station.

RESEARCH SUMMARY

Phloem samples taken from 86 healthy lodgepole pine trees at three points in the 1975 growing season were analyzed for content of dry matter, starch, various forms of sugar and nitrogen, and of selected monoterpenes. Means for July 10 and 31 were significantly lower than those of June 6 for dry matter, soluble reducing sugars, nitrogen, and monoterpenes. Starches and other sugars were higher. β-phellandrene was, by far, the most prevalent of the monoterpenes. Dry matter in the phloem contained an extremely small amount of monoterpene by weight but, of this, individual monoterpenes were distributed in about the same proportions found in pure oleoresin by other researchers. Monoterpene contents from the last (July 31) samples were significantly, although weakly, related to the linear positive effects of phloem thickness and radial growth. An interactive hypothesis is developed for terpene content as a function of phloem thickness, radial growth, and tree diameter. Here, high concentrations of monoterpenes coincide with larger tree diameters, the expected region of high mountain pine beetle survival.

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INTRODUCTION

The role of food quantity in mountain pine beetle (MPB) population dynamics in lodgepole pine is well-documented in the literature. The thickness of phloem within trees in a stand determines whether the insect can prosper there. Beetles tend to select trees that possess the thickest phloem in a stand where trees have similar diameters, and they often select that portion of an individual tree having the thickest phloem (Roe and Amman 1970). The mountain pine beetle is food-limited in those stands of lodgepole pine where developmental temperatures are optimum (Cole and Amman 1969). When beetles have killed most of the larger, thick-phloem trees, they are forced to attack and raise brood in the smaller residual trees. These trees have reduced capacity for supporting brood development because of generally thinner phloem. Subsequently, the population declines (Cole and others 1976).

While the role of phloem quantity in beetle population dynamics is well documented, that of phloem quality is not. Smith (1965) has shown that vapors of the monoterpenes from western white pine (*Pinus ponderosa*) vary in toxicity to the western pine beetle (*Dendroctonus brevicomis*) in the following descending order: limonene > Δ_3-carene > myrcene > β-pinene ~ β-pinene > control. The monoterpene composition of oleoresin in lodgepole pine (*Pinus contorta* var. *muriayana*) was: β-phellandrene, 69.4 percent; α-pinene, 6.4 percent; Δ_3-carene, 8.9 percent; β-pinene, 5.7 percent; myrcene, 3.9 percent; camphene, 0.5 percent; limonene, 2.4 percent; sabinene, 2.1 percent; and α-phellandrene, 0.7 percent (Smith 1964).

In most terpene studies where a variety of pine species were considered, cortical oleoresin differed qualitatively between species but not within species. Coyne and Keith (1972) found no distinct differentiation, either qualitatively or quantitatively, between monoterpene composition of loblolly (*P. taeda*) and slash (*P. elliotii*) pines within or outside of known southern pine beetle outbreaks. Monoterpenes provide bases for distinguishing host species but not for distinguishing resistant trees from check trees (Coyne and Critchfield 1974). Hanover (1975) identified an apparent genetic hierarchical regulation of the major terpene fractions in lodgepole pine. These discrete genetic variations may relate to pest (insect) behavioral patterns, as indicated by differing resistance levels of trees to their respective pest species.

A continuing question is whether tree-to-tree differences in phloem constituents, particularly the monoterpenes, are coincident with the characteristic MPB attack and survival pattern. Alpha-pinene has been the usual monoterpene used in experimentation with pheromones and beetle behavior. However, Moeck (1980) mentions that α-pinene is not an effective pheromone component in lodgepole pine. While peripheral information has been developed in this study, the emphasis has been on monoterpene content of the phloem and its relation to tree characteristics previously found to be linked to MPB population dynamics.

MATERIALS AND METHODS

We took three 5.08 by 5.08 cm phloem samples at breast height from each of 86 uninfested trees distributed over 20 acres (8.1 ha) on the Cache National Forest in 1975. Trees ranged from 12.7 to 50.8 cm in diameter at breast height (d.b.h.). Samples were taken three times during the season: June 6, July 10, and July 31. The samples were transported to the laboratory and frozen on the same day they were removed from the trees. Two samples per tree were analyzed as described later, and one sample stored (frozen) as a backup sample.

The samples were stored in the lab at −25° C. Each of the first two phloem samples were separated from the bark and ground in a Wiley grinder at 20-mesh size by freezing the sample in liquid nitrogen and by passing large amounts of dry ice through the grinder to keep the grinder cold.

Soluble nitrogen and soluble sugars were extracted with 80 percent ethanol. Insoluble products underwent chemical digestion in order to convert them into a soluble form that could be analyzed. Insoluble nitrogen in the sample was converted to ammonia by repeated digestion with a 20 percent sulfuric acid and cleaned with hydrogen peroxide (Hodges and others 1968).

To analyze terpenes, 0.2 to 0.3 g of the ground phloem was placed in a vial with 2 ml of isopropyl ether (free of alcohols, chromatoquality reagent) in a sealed vial and shaken for at least 2 days. We then put 10 microliters of this solution in a Varian Aerograph series 1700 gas chromatograph with a flame ionization detector. The identification and quantity of each component was determined by running dilute standards of the pure components. The peaks were cut out, and the quantity of each component determined from its peak weight. We used a 1.83-m column packed with Porapack Q because the water in the sample from the phloem did not affect this column packing. The injector temperature was 275° C, detector temperature 250° C, carrier gas (high purity helium) 40 psi, and column temperature was programmed from 50° to 250° C at 10° per minute. Ultra high purity hydrogen and air were used for hydrogen detection.

Laboratory analysis was focused on monoterpenes, soluble nitrogen, total nitrogen, reducing sugars, starches, pentoses, and hexoses. Nitrogen was analyzed by the colorimetric Nessler Method (Jacobs 1965). Insoluble nitrogen was determined as the difference between total nitrogen and soluble nitrogen. Sugars, hexoses, and pentoses were determined at the same time with the cysteine and sulfuric acid general reaction on carbohydrates (Dische 1955). Their absorption spectra were then read at 320 mu and 405 mu, which allows the determination of both sugars. Reducing sugars were determined by methods discussed in Dische (1955). Starches were hydrolyzed and then determined by the same procedure as the sugars.

DATA ANALYSIS

Presented in table 1 are average percentages of the phloem (by weight) and associated standard deviations found in dry matter, sugars, starch, nitrogen, and monoterpenes for the trees sampled. Means for June 6 were compared statistically with comparable means at (a) July 10 and (b) July 31.

To establish possible links between tree characteristics and phloem constituents, the latter were fitted as linear functions of all combinations of six pertinent tree characteristics: d.b.h., percent crown length of total tree height, height, phloem thickness, average radial growth for the 5 years prior to sampling, and age.

Results of the regression screen are summarized in table 2 and show that rather weak regression information (R^2) was developed throughout. The July 31 monoterpenes were, however, most strongly related to the tree characteristics evaluated. While even the strongest of these, phloem depth and growth, seem of marginal strength ($0.14 \leq R^2 \leq 0.34$), they do confirm the presence of associated linear, positive increases in monoterpenes. The results provide an information base necessary to the development of more advanced hypotheses, to be evaluated with new data when available. In this case, an interactive hypothesis was developed from the July 31 data. We used two of the variables exhibiting the strongest linear effects (phloem thickness and growth) and one weak variable (d.b.h.) that proved reasonably strong in past MPB dynamics models.

Table 1.—Selected lodgepole pine phloem constituents, percent by weight.

Constituent	June 6		July 10		July 31	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
	------ Percent of total phloem weight ------					
Dry matter	54.6	12.7	45.2	4.1	41.4	4.3
	-Percent of phloem dry matter weight-					
Soluble pentoses	2.0	.56	6.0	1.16	4.7	1.02
Soluble hexoses	1.5	.43	4.3	.61	6.3	1.18
Total	3.5	.96	10.3	1.61	11.0	1.74
All pentoses	3.7	.98	11.4	2.72	8.2	1.44
All hexoses	2.7	.81	7.8	1.60	11.6	2.97
Total	6.4	1.62	19.2	3.57	19.8	3.30
Soluble reduced sugars	3.3	1.70	2.2	.82	1.8	.82
Starch	3.0	1.01	9.0	3.18	8.8	2.97
Insouble nitrogen	.13	.04	.11	.02	.11	.02
Total nitrogen	.18	.07	.13	.03	.12	.03
Monoterpenes						
α-pinene	.052	.058	.039	.033	.030	.026
β-phellandrene	.203	.277	.140	.124	.144	.127
3-terpenes (3-carene + myrcene + α-pinene)	.120	.192	.077	.067	.064	.054
Total	.375	.447	.256	.203	.238	.191

Here, "total terpene" data for July 31 were partitioned over the ranges of phloem thickness, tree growth, and tree d.b.h. and were explored graphically for interactive effects. The data appeared to support a three-way interaction characterized by: positive, shallow concave-upward effects for phloem thickness and growth; a more-or-less bell-shaped effect for d.b.h., maximizing at about 10.5 inches (26.67 cm); and convergence to zero with low growth and phloem thickness. The d.b.h. effect is not oriented at zero but is not meaningful at zero anyway. These effects were in general accord with the mountain pine beetle preference for larger, more vigorous trees, although the rather strong negative trend in terpene content for larger trees — d.b.h. > 10.5 inches (26.67 cm) — was not. Nevertheless, d.b.h. was retained in the model and the resulting four-dimensional relation was formulated mathematically using the techniques specified by Jensen (1973, 1976, 1979) and Jensen and Homeyer (1970, 1971), and was refitted to the data set from which it was partially derived, by weighted[1] least squares. The final hypothesized form ($R^2 = 0.39$, $s_{y \cdot x} \doteqdot 0.15$) is shown graphically in figure 1 and mathematically in appendix table 7.

[1]Variance about the initial model $\hat{Y}$ was expressed as a function of $\hat{Y}$. The inverse of this, $1/\hat{Y}^{2\,7}$, was used as the fitting weight.

Table 2.—Summary of significant (Pr 0.05) coefficients of determination (R^2) for the linear regression screens of independent variables for three sampling dates

Date and independent variable	Main effects[1]							Terpenes			
	Dry matter	Soluble pentoses	Soluble hexoses	Total soluble sugars	Total pentoses	Starch	Total nitrogen	Total	α-pinene	β-phellandrene	β-pinene + carene + myrcene
	Coefficient of determination (R^2)										
JUNE 6											
Diameter at breast height (D)											
Length of crown, % of total								0.12	0.08	0.10	0.12
Height											.05
Phloem thickness (P)								.18		.13	.09
Growth, average annual 5-yr. radial (G)			0.06	0.05				.28	.11	.24	.15
Age		0.05	.07	.06			0.05	.07		.08	.09
								Additive effects			
							P, G	.30	.11	.25	.16
							P, G, D	.30	.12	.26	.18
JULY 10											
Diameter at breast height (D)											
Length of crown, % of total											
Height						0.07					
Phloem thickness (P)			.12	.08			.06	.07	.07	.07	.07
Growth, average annual 5-yr. radial (G)			.05	.04							
Age			.09	.05		.06					
								Additive effects			
							P, G	.07	.07	.07	.07
							P, G, D	.10	.10	.10	.10
JULY 31											
Diameter at breast height (D)								.06		.08	.07
Length of crown, % of total			.08		.10			.18		.18	.18
Height						.04					
Phloem thickness (P)	.06	.04		.06				.30	.18	.34	.26
Growth, average annual 5-yr. radial (G)			.07	.07			.08	.24	.14	.26	.26
Age	.10										
								Additive effects			
							P, G	.35	.21	.39	.34
							P, G, D	.35	.22	.39	.34

[1]Total hexoses and total sugars were screened with nonsignificant results.

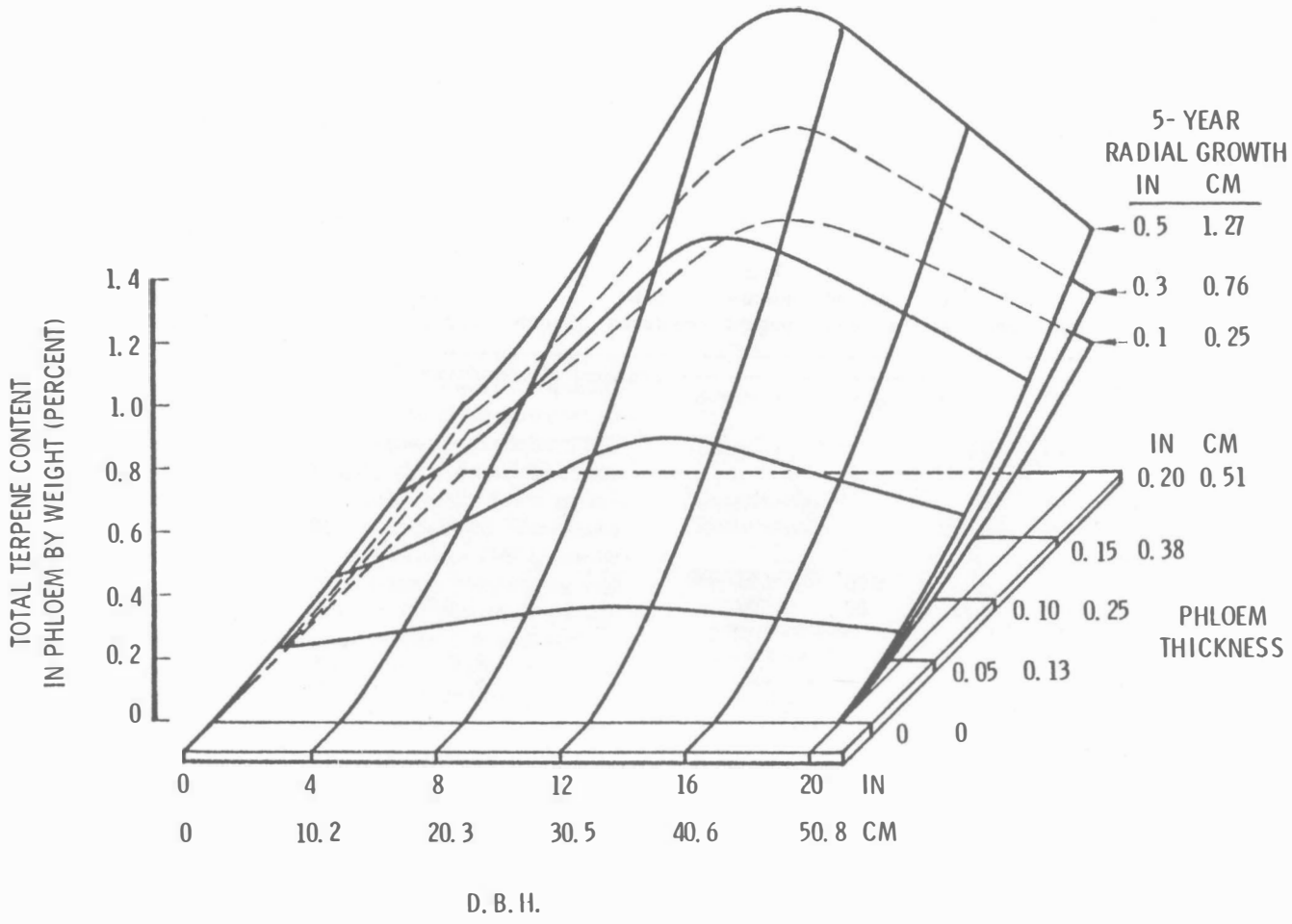

Figure 1. — Hypothesis: total monoterpene percentage of lodgepole pine phloem dry weight, as a function of d.b.h., phloem thickness, and average radial growth.

The July 31 monoterpene percent of phloem dry weight in trees ranged from 0.03 to 1.10 percent. Almost 40 percent of the variance ($R^2 = 0.39$) about the mean of 0.238 was explained by the regression of monoterpene percent on the strongly interacting independent variables, phloem thickness, growth, and tree diameter (fig. 1).

The unexpected bell-shaped effect over d.b.h. is somewhat deceptive because there is a rather strong correlation between phloem and d.b.h. The d.b.h. effect is better characterized by the monoterpene trace over the d.b.h.-phloem line of correlation (fig. 2). There it can be seen that monoterpene content reaches a maximum at about 13 inches (33 cm) and, although the trend is slightly down thereafter, content at 20 inches (51 cm) still exceeds that for 8-inches (20 cm) trees.

Component monoterpenes were explored with much the same results as for the monoterpene sum. So, the mathematical **form** for the sum was adopted for the components and was scaled to the data for each component using weighted ($1/\hat{Y}^{2.7}$) least squares (fig. 3). The coefficients for component models were subsequently adjusted to equal, in sum, that for the all-component model. As a result, contents for the sum of components equal that of the all-monoterpene model at all combinations of d.b.h., phloem, and growth.

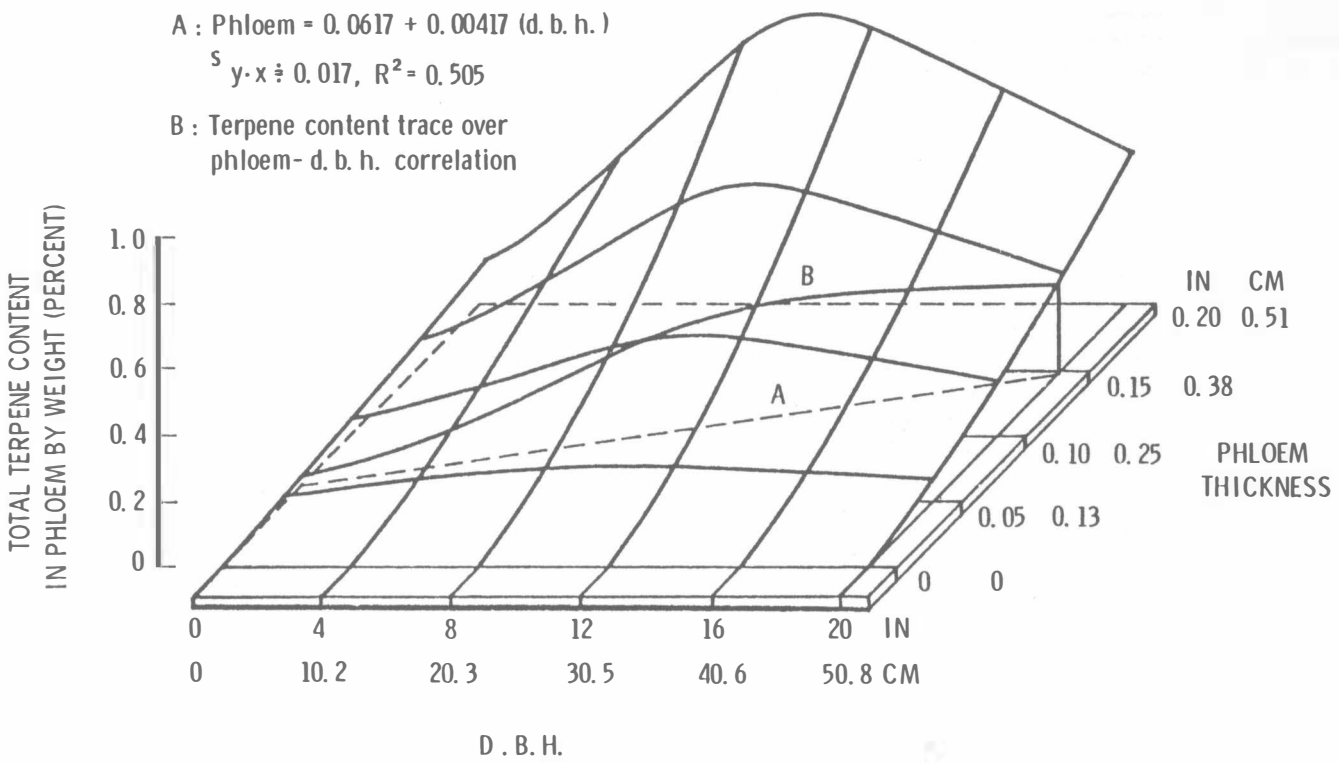

Figure 2. — Hypothesis: total monoterpene percentage of lodgepole pine phloem dry weight, trace over d.b.h./phloem correlation at average annual radial growth (0.159 inches, 0.404 cm).

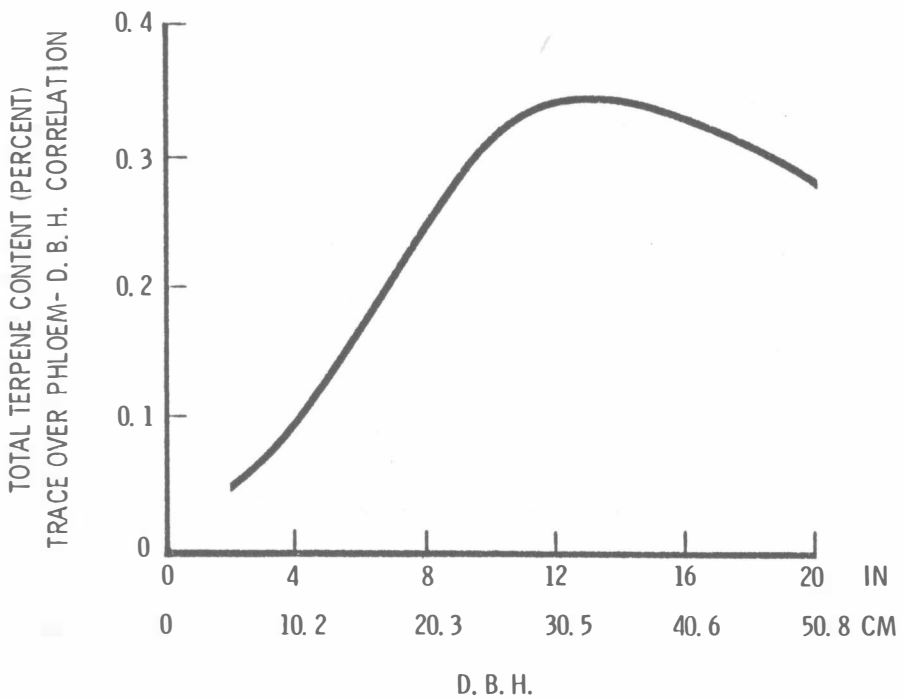

Figure 3. — Hypothesis: total monoterpene percentage, of lodgepole pine phloem dry weight over d.b.h. and phloem thickness at average annual radial growth (0.159 inches, 0.404 cm).

RESULTS

Means and associated standard deviations are shown in table 1 for all phloem contents evaluated in this study. Numbers of sample trees varied from 79 to 86 depending on date of sample and phloem component analyzed.

Means for July 10 and 31 were consistently lower than those of June 6 for dry matter, soluble reducing sugars, nitrogen, and monoterpenes. Differences were significant ($Pr < 0.05$) for the first three components and less so for the monoterpenes ($0.10 \leq Pr \leq 0.05$). Starches and other sugars showed increases from June 6 ($Pr < 0.05$).

We found monoterpene percentage of the phloem dry weight to be extremely small (0.238) and, of this, individual monoterpenes were distributed in about the same proportion as found by Smith (1964) in "pure" oleoresin (table 3). And, in either case, β-phellandrene is by far the largest monoterpene component, followed by the 3-terpene group and α-pinene, respectively. Note that the averages are greater in larger trees with thicker phloem (and vice versa) according to the interactive hypothesis (fig. 1). Too, the expected trend over the d.b.h.-phloem trace (fig. 2) increases to a peak at about 13 inches (33 cm) d.b.h., decreasing thereafter to a low at 20 inches (51 cm) comparable to that at about 9 inches (23 cm).

Note that the percentages of phloem dry weight reported in table 1 and in figures 1 through 3 are based on the monoterpenes measured in this study only. A small reduction in percentages for components could be expected with upward adjustment of the monoterpene sum by 6 percent, to achieve comparability to Smith's (1964) percentages (table 3).

Table 3.—Proportional distribution of monoterpenes: "pure" oleoresin versus phloem dry matter

Monoterpenes	In "pure" oleoresin (Smith 1964)	In phloem dry matter this study, 7/31/75[1]
	Percent by weight	
α-pinene	6.4	11.9
β-phellandrene	69.4	57.0
3-terpenes (3-carene + myrcene + α-pinene)	18.5	25.4
Others (camphene + limonene + sabinene + α-phellandrene)	5.7	(5.7)
Total	100.0	100.0

[1]Original percentage adjusted for 5.7 percent of "others" not evaluated.

DISCUSSION

The inference limitations in this study are rather servere because the sample trees involved are from a single, infinitely small stand relative to the whole. But in the absence of stronger information on lodgepole pine phloem, our findings provide a data-base opportunity to develop hypotheses for more extensive study.

Table 1 contains mean percentages and standard deviations for a variety of phloem components, all of which are likely to have some impact on MPB population dynamics. The data on sugars, starch, and nitrogen are simply documented here for general interest. We note, however, that most sugars and starch are at low levels in the spring and that soluble reducing sugars, nitrogen, and monoterpenes are relatively high. These trends follow expectations based on seasonal tree physiology, but because all but monoterpene relations to tree characteristics appeared to be extremely weak (table 2), we did not attempt to develop such information further.

Respective (but very low) concentrations of monoterpenes in the phloem are parallel in proportions of the monoterpene sum to those found by Smith (1964) in pure oleoresin produced in lodgepole pine (table 3). Beta-phellandrene in both studies proved to be, by far, the largest component of the monoterpenes, and so might easily have the greatest impact on MPB activities. We note that while α-pinene has been found to be an effective pheromone in western white pine, it is not for lodgepole (Moeck 1980).

But whether it is β-phellandrene or some lesser component of the monoterpenes, concentrations in the phloem appear from the hypothesis developed (fig. 2), to increase with tree vigor and size, up to an optimum d.b.h. of about 13 inches (33 cm).

It has been established from past research that threshold diameters in lodgepole pine for successful MPB reproduction are generally in the 8-inch (20-cm) to 9-inch (23-cm) range. And reproduction success is known to be high in larger, more vigorous trees. This information, together with the coincidence of relatively high monoterpene content for larger trees (9-inches [23-cm] to 20-inches [51cm] d.b.h.; see fig. 3), is perhaps suggestive of an attractant role for any one or all of the monoterpenes. It would also appear that monoterpene toxicity levels studies by Smith (1965) are apparently not being reached in the phloem, based on the level of MPB success in larger trees.

The hypothesis developed in this study (fig. 1-3 and appendix) should help to identify points of future study emphasis and may be rescaled (as a unit) and evaluated for performance on new data sets (Jensen 1979).

APPENDIX

Table 4.—Hypothesis values for figure 1. Monoterpene percentage of lodgepole pine phloem dry weight. All-monoterpene % = 1.10301 * (model)[1]

Average annual radial growth		Phloem thickness		D.b.h. 4 10.2	8 20.3	10.5 26.7	12 30.5	16 40.6	20 50.8	*(inches)* *(cm)*
Inches	*cm*	*Inches*	*cm*							
0.1	0.25	0.05	0.13	0.045	0.084	0.094	0.090	0.070	0.049	
		.10	.25	.130	.246	.276	.263	.204	.143	
		.15	.38	.244	.463	.516	.492	.382	.268	
		.20	.51	.381	.723	.807	.769	.597	.418	
.3	.76	.05	.13	.060	.114	.127	.122	.094	.066	
		.10	.25	.176	.335	.374	.356	.277	.194	
		.15	.38	.330	.627	.700	.668	.518	.363	
		.20	.51	.516	.979	1.094	1.043	.810	.567	
.5	1.27	.05	.13	.081	.154	.172	.164	.127	.089	
		.10	.25	.238	.451	.504	.480	.373	.261	
		.15	.38	.446	.846	.945	.901	.699	.490	
		.20	.51	.695	1.321	1.476	1.407	1.092	.765	

[1]The enclosed areas are represented by one or more data points. The same is true for the monoterpene component tables that follow.

Table 5.—Hypothesis values for monoterpene components, percentage of lodgepole pine phloem dry weight (no related figure in text)

Average annual radial growth		Phloem thickness		D.b.h. 4 10.2	8 20.3	10.5 26.7	12 30.5	16 40.6	20 50.8	*(inches)* *(cm)*
Inches	*cm*	*Inches*	*cm*							
				*α-pinene % = 0.15787 * (model)*						
0.1	0.25	0.05	0.13	0.007	0.012	0.014	0.013	0.010	0.007	
		.10	.25	.019	.036	.040	.038	.029	.020	
		.15	.38	.034	.066	.074	.070	.055	.038	
		.20	.51	.055	.014	.115	.110	.085	.060	
.3	.76	.05	.13	.008	.016	.018	.017	.014	.009	
		.10	.25	.025	.048	.053	.051	.040	.028	
		.15	.38	.048	.090	.100	.096	.074	.052	
		.20	.51	.074	.139	.157	.149	.116	.081	
.5	1.27	.05	.13	.011	.022	.025	.023	.018	.013	
		.10	.25	.034	.064	.072	.069	.053	.037	
		.15	.38	.064	.122	.135	.129	.100	.070	
		.20	.51	.100	.189	.211	.201	.156	.109	
				*β-phellandrene % = 0.64292 * (model)*						
0.1	0.25	0.05	0.13	0.026	0.049	0.055	0.052	0.041	0.028	
		.10	.25	.075	.144	.161	.153	.119	.083	
		.15	.38	.142	.270	.301	.287	.223	.156	
		.20	.51	.221	.420	.470	.449	.348	.244	
.3	.76	.05	.13	.035	.066	.074	.071	.055	.039	
		.10	.25	.102	.194	.218	.208	.161	.113	
		.15	.38	.192	.365	.408	.389	.302	.212	
		.20	.51	.300	.571	.637	.608	.472	.330	
.5	1.27	.05	.13	.047	.090	.100	.096	.074	.052	
		.10	.25	.138	.263	.293	.280	.217	.152	
		.15	.38	.260	.493	.551	.525	.408	.285	
		.20	.51	.406	.770	.860	.820	.637	.446	
				*(β-pinene + 3-carene + myrcene) % = 0.30222 * (model)*						
0.1	0.25	0.05	0.13	0.012	0.023	0.026	0.025	0.019	0.013	
		.10	.25	.035	.068	.075	.072	.056	.039	
		.15	.38	.067	.126	.141	.135	.105	.073	
		.20	.51	.105	.198	.221	.211	.164	.115	
.3	.76	.05	.13	.017	.032	.035	.033	.026	.018	
		.10	.25	.049	.091	.102	.098	.076	.053	
		.15	.38	.090	.172	.192	.183	.142	.099	
		.20	.51	.141	.269	.300	.286	.222	.155	
.5	1.27	.05	.13	.022	.043	.047	.045	.035	.024	
		.10	.25	.066	.124	.139	.132	.102	.072	
		.15	.38	.122	.231	.259	.247	.192	.134	
		.20	.51	.191	.362	.405	.385	.299	.210	

Table 6.—Hypothesis values for figures 2 and 3. Monoterpene percentage of lodgepole pine dry weight, at average annual radial growth = 0.159 inches (0.404 cm), average for 86 trees. Percent by weight of phloem at average annual radial growth = 0.159 inches (0.404 cm)

Component	Phloem thickness		D.b.h. 4 10.2	8 20.3	10.5 26.7	12 30.5	16 40.6	20 50.8	*(inches) (cm)*
	Inches	*cm*							
α-pinene	0.05	0.13	0.007	0.013	0.015	0.014	0.011	0.008	
	.10	.25	.020	.038	.043	.041	.032	.022	
	.15	.38	.038	.072	.081	.077	.060	.042	
	.20	.51	.059	.113	.126	.120	.093	.065	
β-phellandrene	.05	.13	.028	.053	.060	.057	.044	.031	
	.10	.25	.082	.157	.175	.167	.129	.091	
	.15	.38	.155	.293	.328	.312	.243	.170	
	.20	.51	.242	.458	.512	.488	.379	.265	
β-pinene + 3-carene + myrcene	.05	.13	.013	.025	.028	.027	.021	.015	
	.10	.25	.039	.074	.082	.078	.061	.043	
	.15	.38	.073	.138	.154	.147	.114	.080	
	.20	.51	.114	.215	.241	.229	.178	.125	
All terpenes (sum of those above)	.05	.13	.048	.092	.102	.098	.076	.053	
	.10	.25	.142	.269	.300	.286	.222	.156	
	.15	.38	.265	.504	.563	.536	.416	.292	
	.20	.51	.414	.786	.879	.837	.650	.455	

Table 7.—Mathematical descriptors for figures 1-3 and appendix tables 4, 5, and 6.

Monoterpene Models

Percent monoterpene content = $(21.0621 * YPP * P^{1.55}) * K_i$

For $D \leq 10.5$

$$YPP = YPD * \left(1.00165 * e^{-\left|\frac{\frac{(D + 8.5)}{19} - 1}{0.395}\right|^2} - 0.00165\right)$$

For $D > 10.5$

$$YPP = YPD * \left(1.07092 * e^{-\left|\frac{\frac{(38.5 - D)}{28} - 1}{0.49}\right|^{1.4}} - 0.07092\right)$$

For $0 \leq D \leq 22$

$$YPD = 0.38 + 1.0292 * G^{1.4}$$

	R^2	$S_{y.x}$ [1]
K_1 = 1.10301, all monoterpenes	0.387	0.150
K_2 = 0.64292, β-phellandrene	0.402	0.098
K_3 = 0.30222, β-phinene + 3-carene + myrcene	0.352	0.044
K_4 = 0.15787, α-pinene	0.213	0.023

where
P = phloem thickness, inches;
D = tree d.b.h., inches;
G = average annual radial growth, last 5 years, inches.

Limits
$0 \leq P \leq 0.25$, $0 \leq D \leq 25$, $0 \leq G \leq 0.5$

[1]Conservative estimates.

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